

***Echidnophaga suricatta* (Siphonaptera: Pulicidae), a new species of flea from the Northern Cape Province, South Africa**

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Echidnophaga suricatta (Pulicidae), a new species of flea collected from the meerkat (*Suricata suricatta* Schreber, 1776) near Garies (30°22'S, 17°31'E) and Brandvlei (30°27'S, 20°29'E), Northern Cape Province, South Africa, is described. Based on chaetotaxy of the tarsal segments, this new species is most closely related to *E. bradyta* Jordan & Rothschild, 1906, *E. iberica* Ribeiro, Lucientes, Osacar & Calvete, 1994, *E. macronychia* Jordan & Rothschild, 1906, and *E. ochotona* Li, 1957. A key is provided for the 23 recognized species or subspecies in the genus *Echidnophaga*.

Key words: taxonomy, morphology, taxonomic key, mammalian ectoparasites, arthropods.

INTRODUCTION

An extensive collection of small mammals and their ectoparasites was made in South Africa in 1969 under the direction of H.W. Setzer, Smithsonian Institution, Washington, D.C. Among the fleas collected was a new species of *Echidnophaga* which is described here.

Hopkins & Rothschild (1953) recorded 17 species or subspecies of *Echidnophaga*. One of these (*E. inexpectata* Smit, 1950) was subsequently placed in a newly erected genus (*Phacopsylla*) by Beaucournu & Horak (1994). Six additional species have since been described. They include *E. ochotona* Li, 1957, *E. tiscadaea* Smit, 1967; *E. calabyi*, *E. eyrei* and *E. octotricha*, all by Mardon & Dunnet (1971), and *E. iberica* by Ribeiro, Lucientes, Osacar & Calvete (1994). Liu & Tung (1962) subsequently described the female of *E. ochotona*. Lewis (1972) presented the distribution and host-parasite relationships of the species of *Echidnophaga*. *Echidnophaga iberica*, whose distribution was not reviewed by Lewis (1972), is a parasite of wild rabbits, *Oryctolagus cuniculus* (Linnaeus, 1758) on the Iberian Peninsula, Spain (Beaucournu 1996). In addition to the new African species described below, other species that occur in Africa include *E. bradyta* Jordan & Rothschild, 1906, *E. aethiops* Jordan & Rothschild, 1906, *E. gallinacea* (Westwood, 1875), *E. larina* Jordan & Rothschild, 1906, and *E. tarda* Jordan, 1925. Twenty-three species are currently recognized in the genus. An updated key to the genus is presented below as seven new

species have been described since Hopkins and Rothschild (1953).

***Echidnophaga suricatta* n.sp., Figs 1–3, 5–9**

Type material. Holotype ♂, ex *Suricata suricatta* Schreber, 1776 (USNM host: 575377), Wallekraal, 40 mi WNW Garies, Northern Cape Province, South Africa, 25 July 1969, O.F. Graupner; Allotype ♀, ex *S. suricatta* (USNM host: 575377), Wallekraal, 40 mi WNW Garies, Northern Cape Province, South Africa, 25 July 1969, O.F. Graupner; Paratypes: 9♂, 5♀, ex *S. suricatta* (USNM host: 575377), Wallekraal, 40 mi WNW Garies, Northern Cape Province, South Africa, 25 July 1969, O.F. Graupner; 4♀, *S. suricatta* (USNM host: 469863), 40 mi WNW Garies, Northern Cape Province, South Africa (30°22'S, 17°31'E), 23 July 1969, O.F. Graupner; 1♀, ex *S. suricatta* (USNM host: 469864) 40 mi WNW Garies, Northern Cape Province, South Africa (30°22'S, 17°31'E), 23 July 1969; 1♂, 1♀, *S. suricatta* (USNM host: 469866), 40 mi WNW Garies, Northern Cape Province, South Africa (30°22'S, 17°31'E), 25 July 1969, O.F. Graupner; 1♂, 4♀, ex *S. suricatta* (USNM host: 469862), 2 mi south Brandvlei, Northern Cape Province, South Africa (30°27'S, 20°29'E), 9 June 1969, S.J. Liversedge. Holotype, allotype and all but seven paratypes are deposited in the National Museum of Natural History, Washington, D.C. Seven paratypes, 2♂, 4♀ with the same data as holotype and 1♂ with the same data as USNM host: 469862 are deposited in the author's collection.

Diagnosis

Echidnophaga suricatta is separable from all known species of *Echidnophaga* except *E. bradyta*, *E. iberica*, *E. macronychia* Jordan and Rothschild, 1906, and *E. ochotona* by the presence of five pairs of stout lateral plantar bristles on the fifth tarsal segments of all legs, from *E. macronychia* by the presence of two spine-like preapical bristles on tarsi V instead of two long, slender hairs (Fig. 3), and from *E. ochotona* by an angular frons. The basal projection of the tarsal claws are also greatly enlarged in *E. macronychia* and only slightly so in *E. suricatta*. Males are distinguished from *E. bradyta* and *E. iberica* by details of the clasper apparatus (Fig. 8): 1) sides of P1 are parallel and the apex is rounded symmetrically; 2) P2 is acutely pointed, and 3) apex of P3 is reflected rearward *vs* forward. Females are similar to *E. bradyta*, but distinguished by the obtusely blunt shape of st. VIII that bears no setae, while *E. bradyta* is pointed with two apicolateral setae (Figs 4, 6). *Echidnophaga suricatta* females differ from those of *E. iberica* by the presence of more than six setae per side on tergum VIII, the ventral proximal area of the bulga of the spermatheca is less strongly ventricose, and the length of segment V of metatarsus is longer (three times its greatest width).

Description

Male. Head (Fig. 1). Frons with thick incrassation from oral angle to heavily chitinized falx. Three minute setae along shallow medial longitudinal groove of frons and three along same groove of occiput (in lateral view). Frontal angle present, but smoothly rounded. Preantennal area with ocular row of two setae and posterior marginal row of occipital area with a single slender seta at ventral margin and a smaller seta at dorsal crest. Eye heavily pigmented, large, and contiguous with dorsal and ventral internal sclerotized ridges. Scape with six or seven setae, pedicel with fringe of long setae extending to apex of clavus. Segments of the clavus are ventrally fused with five lateral minute setae dorsad of ventral margin (females with only four setae). Antenna partially ensheathed in antennal fossa by genal process. Genal lobe well developed. Maxillary palpus of four segments, last twice length of third segment, and extending to apex of procoxa. Maxilla well developed, subacute. Epipharynx and lacinia extending three-quarters length of procoxa, latter only moderately serrate.

Thorax (Fig. 2). Six setae per side on pronotum,

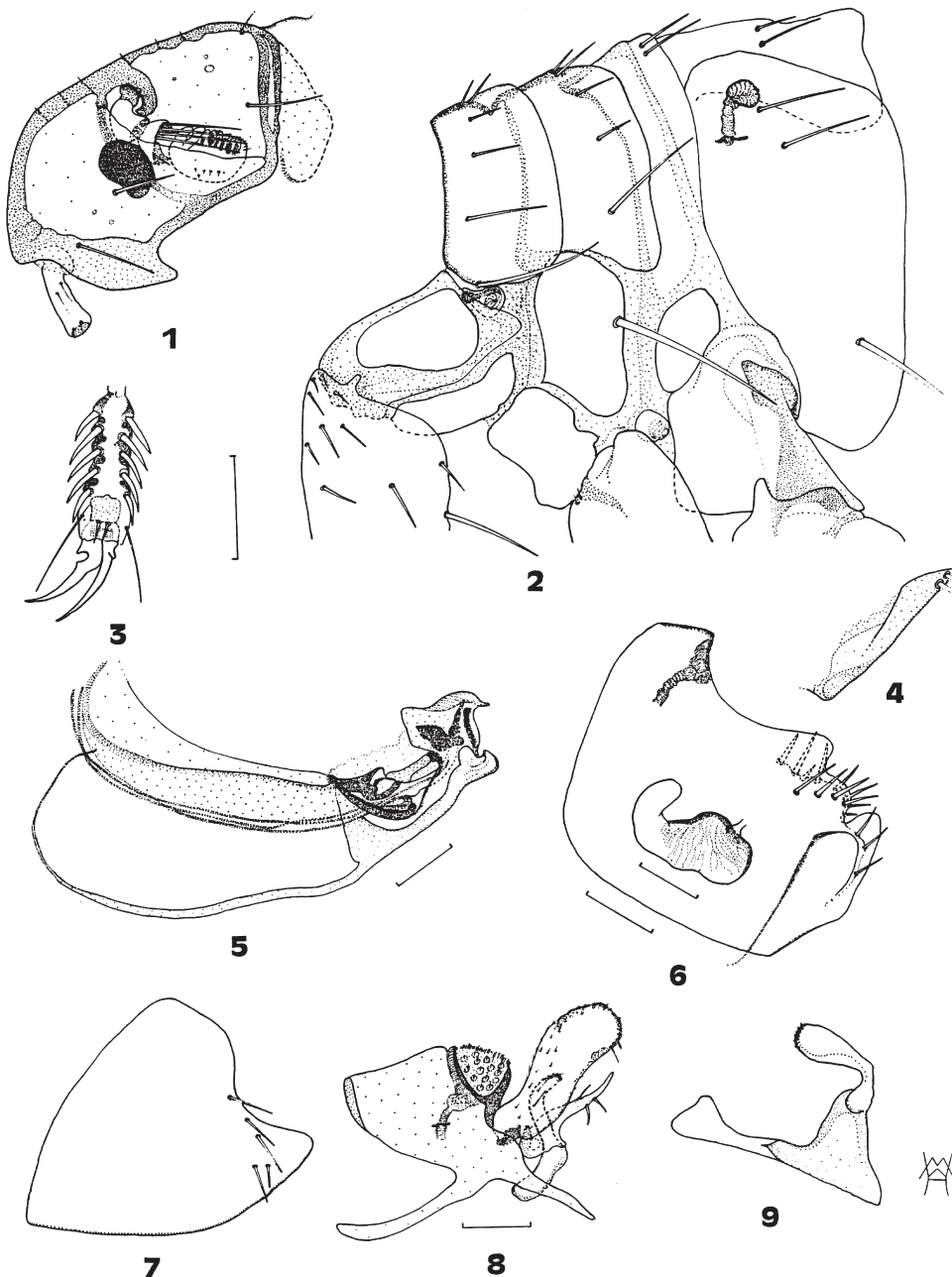
five on mesonotum and two on metanotum. Proepisternum with posterior lobe somewhat developed, prosternum reduced and inconspicuous, proepimeron without setae. Pro-, meso- and metasternites lack setae. Mesepimeron with large seta on posterior margin. Metepisternum without setae. Pleural arch and pleural ridge well developed. Metepimeron bearing two setae below circular spiracular fossa and a single larger seta on ventral third of sclerite.

Legs. Procoxa with 17–18 lateral setae (including marginals), one especially large seta at middle posterior margin. Anterior margin of ventral three-quarters of mesocoxa with anteroapical tooth, 18–20 slender setae on anterior margin, five stout lateral setae dorsad to apical tooth, dense patch of 20–26 stout spiniform bristles on mesal apical third and two stout setae on apex near articulation with trochanter. Lateral bristle, guarding femoral-tibial joint, longer than medial bristle on fore femur and shorter than medial bristle on mid and hind femora. Three minute lateral setae and one mesal seta on fore femur, ten fine setae along dorsal margin. A single stout ventrally directed seta on distoventral margin of fore and mid femora. Ten to 12 setae along dorsal margin of mid and hind femora. Two lateral setae on proximal quarter of mid femur and row of 10 setae extending from base of hind femur to apex on mesal surface. Dorsal notches of fore, mid, and hind tibia, 4, 5, 5, respectively, no mesal or lateral setae. Measurements of tibia and segments of tarsi (tarsal claws and petioles excluded) of holotype given in microns.

Leg	Tibia	Tarsal segments				
		I	II	III	IV	V
Pro	200	53	50	45	38	150
Meso	275	83	103	68	48	153
Meta	450	243	140	88	65	163

Segment V of all tarsal segments with five lateral plantar bristles, two preapical plantar bristles and two preapical lateral hairs (Fig. 3).

Unmodified abdominal segments. Tergum I bearing two setae per side, tergites II–VI with one per side, and tergum VII with three per side (only two per side in female) and a single antesensorial bristle. All setae of tergites far dorsad of spiracular fossae. Male sternites II–VI without setae and VII with one per side. Female sternites II–III without setae, IV–VI with one per side and VII varying from one to three per side.



Figs 1–9. *Echidnophaga suricata*, n.sp. 1, Head, male holotype; 2, thorax, male holotype; 3, metatarsus V, male paratype; 4, *Echinophaga bradyta*, female, eighth sternum. 5–9: *E. suricata*, paratypes; 5, aedeagus; 6, spermatheca, eighth tergum and eighth sternum; 7, eighth sternum, male; 8, ninth tergum and clasper; 9, ninth sternum, male. Scales bars = 100 μ m.

Modified abdominal segments of male (Figs 7–9). Sensilium with 14 trichobothria (pits) per side. Manubrium narrow, apodeme of ninth tergum broadly expanded anteriorly and extending

postad of P3. P1 of clasper 3.4 times as long as its greatest width and extending nearly twice the length of P2, or P3. P2 acutely pointed, bearing three setae, one dorsad and two ventrad. P3 with

well-developed basal apodeme, process with parallel margins and sclerotized apex reflected caudally. Eighth sternum large, enveloping aedeagus, sternum IX and base of clasper apparatus. Six setae are arranged in a horizontal row below a concavity on dorsal margin. Tergum VIII reduced. Dorsal arm of sternum IX club-like with apical fringe of minute setae. Proximal arms fused at the acute basal angle and connected about half-way towards apex by a membrane. The membrane cradles ventral wall of aedeagal pouch and end chamber.

Aedeagus (Fig. 5). Median dorsal lobe reticulate along thickened apical margin. Apodemal rod arising from heavily sclerotized ventral wall of aedeagal pouch extends anterior to at least the apex of aedeagal apodeme. Sclerotized inner tube long, narrow and reflected upward, terminating just beneath median dorsal lobe. Ford's sclerite and crochet sclerotized. Virga ventralis arising from vesicle extends slightly beyond middle of aedeagal apodeme.

Modified abdominal segments of female (Fig. 6). Posterior margin of tergum VIII undulate with three lateral lobes and a small lobe mesally. Mesal lobe bears five stout setae, middle lobe 6–8 setae, and ventral lobe three setae. Sternum VIII is reduced and bluntly club-shaped. Spermatheca similarly shaped as in other species of *Echidnophaga*, with little differentiation between bulga and hilla. Posterior margin of sternum VII entire, without lobes or sinuses.

Dimensions (slide mounted specimens). Male, average length 1.7 mm ($n = 11$), female, average length 1.8 mm ($n = 16$).

Other material examined. Specimens from the Rothschild Flea Collection, British Museum (Natural History): 1♀, ex: *Suricata* sp., Villiers, Orange Free State, South Africa, 29 May 1936, Bryden and 1♀, ex: *Herpestes badius* = *Galerella sanguinea* (Ruppell, 1836), Wakkerstroom, Transvaal, South Africa, March 1904, C.H.B. Grant. It should be noted that the spermatheca of the specimen from Villiers was illustrated as *E. bradyta* in Plate 17, Fig. D, in Hopkins & Rothschild (1953). Robert E. Lewis Collection and National Museum of Natural History, Washington, D.C.: 1♀ each, ex: 'Suricats yellow mongoose & ground squirrel', Orange Free State, South Africa, 1925–26, B. De Meillon.

Etymology. The species is named after the meerkat species *S. suricata* that appears to be the primary host. The name was selected as a noun in apposition.

Key to the known species of *Echidnophaga*¹

1. Fifth tarsal segment with a single lateral plantar bristle. Two additional pairs of minute bristles are present and set on to plantar surface (western Australia) . . . *E. liopus*
— Two or more stout lateral plantar bristles . . . 2
2. Fifth tarsal segment with two stout lateral plantar bristles, a third, minute or hair-like bristle may be present 3
— Three or more stout lateral plantar bristles (Fig. 3) 5
3. Mouthparts at most reaching fore coxa, incrassation below frontal angle of frons thickened ventrally, flange of prosternum approaching a right angle (southern Australia) *E. octotricha*
— Mouthparts reaching well beyond fore coxa, incrassation below frontal angle of frons with massive posterior bulge, lobular flange of prosternum extended postad forming an obvious acute angle 4
4. Stout lateral plantar bristles on fifth tarsal segment close together, and proximal to middle of segment (eastern Australia) *E. ambulans ambulans*
— Stout lateral plantar bristles widely separated, distal pair very near middle of segment (western Australia) . . . *E. ambulans inepta*
5. With at most three pairs of stout lateral plantar bristles 6
— Four or more stout lateral plantar bristles (Fig. 3) 12
6. Fifth tarsal segment with second lateral plantar bristle much nearer first than third lateral plantar bristle; bulga of spermatheca globular, demarcation of hilla and bulga obvious (East Africa from Ethiopia to South Africa) *E. larina*
— Second lateral plantar bristle about equal distance between first and third (Fig. 3); bulga not globular and demarcation of hilla and bulga confluent and indistinguishable . . 7
7. Genal lobe hook-like, apex pointing somewhat forward (southern Australia) . . *E. cornuta*

¹This key is partially adapted from those of Hopkins & Rothschild (1953) and Dunnet & Mardon (1974). Numbers of lateral plantar bristles on the fifth tarsal segments are used extensively throughout the key as a distinguishing character. Characteristic of the genus, these bristles are typically robust proximally, each pair diminishing in size toward the distal end of the tarsi. For the purposes of this key, distal bristle(s) differing only slightly in size from adjacent proximal bristles are counted as lateral plantar bristles, whereas those that are distinctly minute or hair-like in comparison, are not counted as lateral plantar bristles, although they occupy the position of such.

- Genal lobe neither hook-like nor pointing forward (Fig. 1) 8
- 8. One strong occipital seta (Fig. 1) (several minute setae may also be present) 9
- Two strong occipital setae 11
- 9. Internal bulging incrassation of frons extends from frontal angle to oral angle (male unknown) (southeast Australia) *E. eyrei*
- Bulging of internal incrassation confined to lower half between frontal angle and oral angle 10
- 10. Entire eye distinctly below level of frontal angle (Australia) *E. perilis*
- Entire eye at same level or above the level of frontal angle (southern Australia) ... *E. calabyi*
- 11. Thick internal incrassation extends from frontal to oral angle; frontal angle sharply angular (Armenia) *E. popovi*
- Internal incrassation tubular with origin at oral angle (Mongolia) *E. tiscadaea*
- 12. Four well-developed lateral plantar bristles present on fifth tarsal segment [exceptional rare populations of *E. gallinacea* may have five (Smit 1977)] 13
- Five well-developed lateral plantar bristles on fifth tarsal segment (Fig. 3) 20
- 13. Sclerotized margin of frons from frontal angle toward occiput homogeneous and complete (Fig. 1) 14
- Sclerotization absent for a short distance from frontal angle towards occiput (Australia) *E. myrmecobii*
- 14. Two preapical plantar bristles present on fifth hind tarsal segment (Fig. 3) (sometimes one or two in *E. murina*) 15
- Only one preapical plantar bristle present on fifth hind tarsal segment (sometimes one or two in *E. murina*) 18
- 15. Preapical plantar bristles long, hair-like, extending well beyond margin of plantar surface (western Australia) *E. aranka*
- Preapical plantar bristles shorter, at most extending just beyond margin of plantar surface 16
- 16. Head obviously longer than high .. *E. murina*
- Length and height of head approximately equal 17
- 17. Occiput without a distinct lobe, vertical diameter of spiracles of eighth tergum longer than second segment of hind tarsus, large species (Ethiopia) *E. tarda*
- Occiput usually with a well-developed lobe in female, spiracle of eighth tergum shorter than second segment of hind tarsus, small species (cosmopolitan) *E. gallinacea*
- 18. Frontal angle absent, frons sloping from sharp oral angle towards occiput (East Africa, Somalia to South Africa) *E. aethiops*
- Frontal angle present 19
- 19. Internal incrassation of frons below frontal angle forming two tubular processes (central Asia) *E. oschanini*
- Internal incrassation blunt and bulbous (circum-Mediterranean with disjunct population in eastern Asia) *E. murina*
- 20. Frons distinctly angular, although angle may be rounded. 21
- Frons smoothly rounded without angular appearance (China) *E. ochotona*
- 21. Claw of tarsus with large basal projection; preapical plantar bristles hair-like (western Australia) *E. macronychia*
- Claw of tarsus with at most a minute basal projection; preapical plantar bristles nearly spiniform. 22
- 22. Males 23
- Females 25
- 23. Penis rods longer than aedeagal apodeme, making a complete coil (Spain) *E. iberica*
- Penis rods shorter than aedeagal apodeme .. 24
- 24. P1 of clasper broadening apically and truncate, P3 reflected anteriorly (South Africa) *E. bradyta*
- P1 somewhat parallel from base to apex and rounded apically, P3 reflected posteriorly (Fig. 8) (South Africa) *suricatta* n.sp.
- 25. Metepimeron bearing four or five setae (Spain) *E. iberica*
- Metepimeron with three setae, two dorsally immediately below spiracle and one ventrally 26
- 26. Eighth tergum with lateral patch of 3–6 setae on at least one side, eighth sternum lightly sclerotized and blunt caudally (Fig. 6) (South Africa) *E. suricatta* n.sp.
- Eighth tergum usually with 0–1 lateral seta, eighth sternum heavily sclerotized and protruding to a point caudally (Fig. 4) (South Africa) *E. bradyta*

DISCUSSION

The type series was collected only from colonial meerkats, *S. suricatta*, that inhabit dry, open country, commonly with hard or stony ground (Smithers 1971). Other recorded associations are probably accidental, but it would not be unex-

pected to find *E. suricatta* occasionally on the thick-tailed or yellow mongoose [*Cynictis penicillata* (G. Cuvier, 1829)] or on African ground squirrels, *Xerus* spp. *Suricata suricatta* frequently associates with *C. penicillata* and *Xerus* spp. in their colonial settings. The distribution of *S. suricatta* extends from southwestern Angola, Namibia, Botswana, and into South Africa. Additional collecting of fleas from *S. suricatta* may extend the distribution of *E. suricatta* beyond its known distribution in South Africa.

Smit (1977) noted occasional specimens of *E. gallinacea* with five pairs of lateral plantar bristles, e.g. South Africa from cat, Senegal from 'brown rat' and an isolated micro-population in Kenya from the white breasted bee-eater, *Merops bullockoides* Smith, 1834, that lives in burrows in earthen banks. Smit suggested that 'structural abnormalities may arise when immature stages of a flea develop in an environment which is foreign for the species concerned.' *Echidnophaga gallinacea* that undergo development in the burrow of the wild rabbit, *O. cuniculus* (abnormal for the species), may express supernumerary lateral plantar bristles ($n = 5$). The chaetotaxy of the fifth tarsal segments of *E. iberica* reported by Ribeiro *et al.* (1994) may be a result of populations of *E. gallinacea* adapting to a new host and environmental situation.

I examined specimens of *Xenopsylla cunicularis* Smit, 1957, and *E. iberica* from the wild rabbit *O. cuniculus* from the Iberian Peninsula. *Xenopsylla cunicularis* can be differentiated from the closely related *Xenopsylla ramesis* (Rothschild, 1904) only by minor differences in the plantar bristles and setation of the plantar surface (similar to differentiation of *E. gallinacea* and *E. iberica*). Although *X. cunicularis* is not the subject of this paper, one might postulate that conditions in the burrows of *O. cuniculus* contribute to a consistent expression of supernumerary bristles, an adaptive feature that possibly has some selective survival advantage for life in the burrow. *Echidnophaga iberica* does differ from *E. gallinacea* by the possession of five lateral plantar bristles instead of four and penis rods that are notably longer; however, other differences seem relatively minor. Additional studies of *E. iberica* (and *X. cunicularis*) may indicate that minor variations in the number of plantar bristles are simply a genetic expression triggered by burrow conditions (similar to the development of supernumerary plantar bristles in *E. gallinacea* in burrows of Kenya's bee-eaters).

Much has been written regarding the theoretical evolution of combs and bristles as a mechanism to enhance the survival of fleas that live on very active hosts (fossorial, scansorial, volant), or those that continually preen themselves to rid themselves of ectoparasites. The author, while engaged in combing hosts or processing alcohol-preserved specimens, has never observed fleas grasping feathers or hairs by somatic setae, nor with their combs (false, genal, pronotal or abdominal). However, the ability of fleas to grasp single barbules or hairs of host animals with their tarsal claws aided by the bristles on the margins and surface of the tarsi, has been commonly observed. The adaptive benefits of tarsal claws and numbers of lateral plantar bristles have received little attention, although Smit (1972) provided an interpretation of some of these adaptive features. The success of a flea to acquire a host during their saltatorial antics and remain attached for the duration of feeding and occasional mating undoubtedly can be attributed to bristles on the plantar surfaces and their opposing tarsal claws. An optimum configuration for these structures is largely host dependent. For example, it is clear that echidnas and/or marsupials are the principle hosts for nine of the 11 Australian species (*E. ambulans* ssp., *E. aranka*, *E. calabyi*, *E. cornuta*, *E. eyrei*, *E. liopus*, *E. macronychia*, *E. octotricha*). The two additional species (*E. myrmecobii*, *E. perilis*) display less host specificity, occurring on a variety of hosts (marsupials included). Eight of the 11 Australian species bear only 1–3 lateral plantar bristles, with *E. aranka*, *E. myrmecobii* and *E. macronychia* bearing four, four and five, respectively. By contrast, of the 11 species occurring in the Palaearctic or Ethiopian Regions, eight have either four or five lateral plantar bristles and three possess only three. *Echidnophaga gallinacea*, the only cosmopolitan species, has four. Fossorial, scansorial or volant hosts (lagomorphs, rodents and bats) that move quickly, appear to harbour species with increased numbers of lateral plantar bristles, e.g. *E. aethiops*, *E. bradyta*, *E. gallinacea*, *E. iberica*, *E. murina*, *E. oschanini*, *E. suricatta* and *E. tarda*, while those that move more slowly (echidnas and marsupials) tend to have fewer, e.g. *E. ambulans* ssp., *E. calabyi*, *E. cornuta*, *E. eyrei*, *E. liopus*, *E. octotricha* and *E. perilis*.

The possession of four or five pairs of lateral plantar bristles is considered a primitive condition and the loss of bristles, a secondary specialization. Since Africa has a preponderance of species with

increased numbers of lateral plantar bristles, this suggests that the genus *Echidnophaga* might have its centre of origin in Africa as proposed by Traub (1980). It should be noted that the primitive condition might (in some situations) provide a selective survival advantage; however, a change of host and/or ecological conditions may trigger evolutionary modifications necessary to enhance survival, e.g. a reduction in lateral plantar bristles.

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REFERENCES

- BEAUCOURNU, J.C. 1996. Notes sur le genre *Echidnophaga* Olliff, 1886 (Siphonaptera, Pulicidae, Pulicine). A propos d'*E. iberica* Ribeiro, Lucientes, Osacar & Calvete 1994, parasite du lapin *Oryctolagus cuniculus*. *Biogeographica* **72**(2): 99–111.
- BEAUCOURNU, J.C. & HORAK, I.G. 1994. *Phacopsylla* gen. nov. for *Echidnophaga inexpectata* Smit, 1950 (Siphonaptera, Pulicidae). *Journal of African Zoology* **108**: 133–241.
- DUNNET, G.M. & MARDON, D.K. 1974. A monograph of Australian fleas (Siphonaptera). *Australian Journal of Zoology*, Suppl. Ser. **30**: 1–273.
- HOPKINS, G.H.E. & ROTHSCCHILD, M. 1953. *An Illustrated Catalogue of the Rothschild Collection of Fleas (Siphonaptera) in the British Museum (Nat. Hist.)*, Vol. I. *Pulicidae and Tungidae*. British Museum (Natural History), London.
- LEWIS, R.E. 1972. Notes on the geographical distribution and host preferences in the order Siphonaptera, Part 1. Pulicidae. *Journal of Medical Entomology* **9**: 511–520.
- LIU, L.C. & TUNG, Y.S. 1962. A morphological description of the female flea *Echidnophaga ochotona* Li, 1957. *Acta Zoologica Sinica* **14**: 141–144.
- MARDON, D.K. & DUNNET, G.M. 1971. Four new pulicid fleas (Siphonaptera) from Australia. *Journal of the Australian Entomological Society* **10**: 123–130.
- RIBEIRO, H., LUCIENTES, J., OSACAR, J.J. & CALVETE, C. 1994. New species of flea (Siphonaptera: Pulicidae) from Spain. *Journal of Medical Entomology* **31**: 887–889.
- SMIT, F.G.A.M. 1972. On some adaptive structures in Siphonaptera. *Folia Parasitologica* **19**: 5–17.
- SMIT, F.G.A.M. 1977. An unusual form of the stick-tight flea *Echidnophaga gallinacea*. *Revue zoologique africaine* **91**: 198–199.
- SMITHERS, R.H.N. 1971. *The Mammals of Botswana*. Museum Memoir No. 4, 1–340. Trustees of the National Museums of Rhodesia, Salisbury.
- TRAUB, R. 1980. The zoogeography and evolution of some fleas, lice and mammals. In: *Fleas*, (eds) R. Traub and H. Starcke, pp. 93–172. Proc. Internat. Conf. Fleas, Ashton Wold/Peterborough, United Kingdom, 21–25 June 1977.